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# Using exclusion rate to unify niche and neutral perspectives on coexistence

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The competitive exclusion principle is one of the most influential concepts in ecology. The classical formulation suggests a correlation between competitor species similarity and competition severity, leading to rapid competitive exclusion where species are very similar; yet neutral models show that identical species can persist in competition for long periods. Here, we resolve the conflict by examining two components of similarity – niche overlap and competitive similarity – and modeling the effects of each on exclusion rate (defined as the inverse of time to exclusion). Studying exclusion rate, rather than the traditional focus on binary outcomes (coexistence versus exclusion), allows us to examine classical niche and neutral perspectives using the same currency. High niche overlap speeds exclusion, but high similarity in competitive ability slows it. These predictions are confirmed by a well-known model of two species competing for two resources. Under ecologically plausible scenarios of correlation between these two factors, the strongest exclusion rates may be among moderately similar species, while very similar and highly dissimilar competitors have very low exclusion rates. Adding even small amounts of demographic stochasticity to the model blurs the line between deterministic and probabilistic coexistence still further. Thus, focusing on exclusion rate, instead of on the binary outcome of coexistence versus exclusion, allows a variety of outcomes to result from competitive interactions. This approach may help explain species coexistence in diverse competitive communities and raises novel issues for future work.

The long-established competitive exclusion principle maintains that, under constant ecological conditions, two species competing for the same resource cannot coexist for long (Grinnell 1904, Volterra 1926, Gause 1932), or more simply, complete competitors cannot coexist (Hardin 1960). More sophisticated formulations have been proposed (Levin 1970, Kalmykov and Kalmykov 2013), but the basic notion has not been modified. A substantial body of research in community ecology has been devoted to explaining the apparent coexistence of numerous very similar species in nature, and many mechanisms have been proposed in this context. The earliest proposition was perhaps Hutchinson's contention that predation and disturbance keep populations away from equilibrium and thus prevent competitive exclusion (Hutchinson 1941, 1961). Other proposed mechanisms include the Janzen–Connell hypothesis (Janzen 1970); the resource-ratio theory (Tilman 1982); environmental variation across space, also termed 'mass effects', (Shmida and Wilson 1985); and storage effects across space (Chesson 1982) and time (Grubb 1977, Chesson 1983, Kalyuzhny et al. 2015). These mechanisms have been reviewed elsewhere (Palmer 1994, Tokeshi 1999, Wright 2002). While these mechanisms are valid, the most fundamental mechanism for species coexistence may be inherent in the nature of exclusion, which may be rather different from what is typically assumed.

Most previous attempts to explain species co-existence have focused on whether both species persist indefinitely (at equilibrium, or another dynamic attractor such as a limit cycle, Chesson 2000, Adler et al. 2007, Mayfield and Levine 2010). However, the outcomes of ecological interactions are not so clearly delineated; competitors might persist together for very long periods although eventual exclusion is predicted, and conversely demographic stochasticity or external disturbances mean that species cannot, in practice, coexist forever. Thus, over ecologically realistic timescales, exclusion rate is arguably the most relevant measure of competitive exclusion, and the dynamics, rather than the long-term outcome of competitive exclusion, should be the focus of research (Hutchinson 1961, Kalyuzhny et al. 2014). Focusing on extinction dynamics rather than classes of outcomes also provides a common thread uniting classical niche and neutral approaches.

The niche-neutral divide in the recent ecological literature (Rosindell et al. 2012, Connolly et al. 2014, Kalyuzhny et al. 2014) corresponds to a division between an approach based on tacitly assumed species differences in resource requirements (niche theory), and one based on an assumption of competitive equivalence (neutral theory). Hubbell's neutral model (Hubbell 2001) demonstrated that even species with identical niches could coexist for very long periods of time, and thus raised the profile of coexistence in circumstances where deterministic theory would predict exclusion. Such findings stood in stark contrast to the clear predictions of niche theory. Many ecologists have suggested that these are ends of a continuum (Gravel et al. 2006, Leibold and McPeek 2006, Adler et al. 2007, Allouche and Kadmon 2009, Chisholm and Pacala 2010, 2011, Haegeman and Loreau 2011, Fisher and Mehta 2014, Kalyuzhny et al. 2014, 2015). However, a mechanistic explanation of the factors that determine the location of communities along this continuum is missing (but see Adler et al. 2007). Here we explore the mechanistic basis of competition and show how it can bridge niche and neutral approaches.

In order for competitive exclusion to occur, two conditions need to be met: 1) niche overlap: competitor species require the same resources (May 1974); and 2) competitive imbalance: one species outperforms the other in capturing and/or utilizing resources (Kramer and Drake 2014). Traditionally, studies of the competitive exclusion principle have focused on the role of niche overlap (Levin 1969, Colwell and Futuyama 1971, Pianka 1974, Schoener 1974, Lawlor and Maynard-Smith 1976, Roughgarden 1976, Tilman and Wedin 1991, Huisman and Weissing 1999, Leibold 1999, Dybzinski and Tilman 2007). It is typically assumed that the severity of competition is positively related to the degree of niche overlap between competitors (Darwin 1859). The effects of niche overlap on competition have been modelled mathematically (Volterra 1926), and tested in classical lab experiments (Gause 1932, Park 1954). The idea became a cornerstone in community ecology (Hardin 1960), and inspired conceptual constructs such as limiting similarity (MacArthur and Levins 1967) and character displacement (Brown and Wilson 1956, Dayan and Simberloff 2005). Experimental results that did not conform with the principle were often dismissed or explained as outliers (Turner et al. 1996, Miller et al. 2011, Beaudrot et al. 2013).

The second component required for competitive exclusion, competitive differences between species, was largely ignored in the classical formulation of the competitive exclusion principle. Hardin, in his influential paper (Hardin 1960) writes 'No matter how small the difference between the competing species in their efficiency in producing offspring may be, one species will eventually replace the other' (p. 1293). However, over the years, a few authors have considered the importance of differences in competitive abilities (Aarssen 1983, Abrams 1986, Zhang and Lin 1997), finding that strongly asymmetrical competition can speed competitive exclusion, but that for very similar competitors, exclusion may be very slow. Support for this notion may be found in a simulation study (Kramer and Drake 2014) where it was found that competitive imbalance was the most important factor affecting time to exclusion. Similarly, a competition experiment found that when both species had similar performance in extracting soil nitrogen, exclusion took longer than when one species was clearly superior in this respect (Dybzinski and Tilman 2007).

In the last decade, several studies (May 1974, Chesson 1990, 2000, Adler et al. 2007, Mayfield and Levine 2010, Carroll et al. 2011, Yenni et al. 2012, Carroll and Nisbet 2015, Shtilerman et al. 2015) have suggested that a framework for species coexistence should include both niche differences (also termed 'stabilization') and competitive differences (also termed 'fitness inequality'). Yet the frameworks proposed in those studies considered only indefinite coexistence and its vulnerability to stochastic extinction (Yenni et al. 2012), giving no attention to the speed of competitive exclusion outside the area of deterministic coexistence.

Here, we introduce a framework where niche difference and competitive differences are combined. At the center of this framework we use the concept of competitive exclusion rate as a quantitative measure of competitive exclusion. We define exclusion rate as the inverse of the expected time until the extinction of one of the competing species, and model it as a function of both niche overlap and competitive inequality, which can vary independently. In this context competitive exclusion becomes very different from its classical conception.

## Conceptual framework

We propose that niche overlap (i.e. the degree to which species rely on the same resources) represents merely the potential for exclusion, the impetus fueling the process of competitive exclusion. The realization of this potential, and thus the actual exclusion rate, is determined by differences between species in their competitive abilities. The greater the similarity between species in their niches (i.e. the more similar they are in their resource preferences), the more severe is the competition (Fig. 1a). If species do not compete for any shared resources, competition severity is 0, and there is no potential for competitive exclusion, whereas if they are identical in their resource usage, competition severity is 1. The realization of the potential for exclusion depends on the relative competitive abilities of the competitor species. The efficiency of the exclusion process is negatively related to the similarity between species in their competitive abilities (Zhang and Lin 1997) (Fig. 1b). In the extreme case where the traits of two species are essentially the same (except they do not reproduce with each other), there is a complete competitive equivalence. In such a case, even though competition severity is intense, the potential for competitive exclusion cannot easily be realized, and the exclusion rate approaches zero.

The actual rate of exclusion is determined by both the potential (competition severity) and its realization (exclusion efficiency). Therefore, a nearly zero exclusion rate is expected for very different species (in their niches) but also for very similar species (in their competitive abilities). This notion opposes the thinking of most community ecologists. The concept of slow exclusion of very similar species was suggested as an outcome of long-term multi-species interactions (Scheffer and Van Nes 2006).

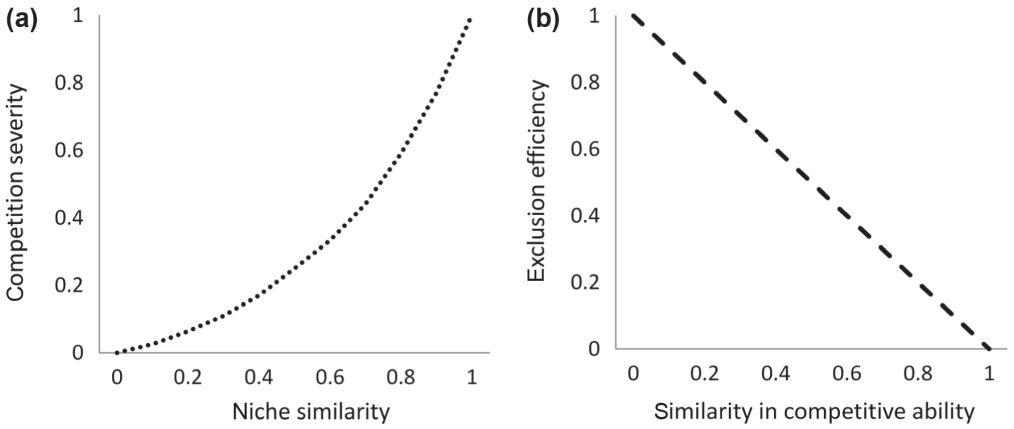


Figure 1. A schematic illustration of (a) competition severity ( = exclusion potential), (b) exclusion efficiency.

If niche similarity and similarity in competitive ability vary independently, then one might predict that they would yield an exclusion rate similar to the form shown in Fig. 2a. Species with identical niches and equal competitive abilities should display effectively "neutral" competition (zone 'A' in Fig. 2a), a scenario that has been widely discussed and modelled in recent years (Hubbell 2001, Haegeman and Etienne 2011, Rosindell et al. 2012). While such competing species can exclude one another, the lack of competitive dominance in such contests turns the dynamics into a zero-sum random walk, and in such a scenario the time to exclusion rises rapidly with community size (i.e. the total population of all competitors). In communities of many thousands or millions of individuals, the time to competitive exclusion becomes extremely large. Note that this well-modelled scenario is for equal competitors with complete niche overlap; the time to exclusion for less severe competitors (niche overlap $< 1$) should be even longer, leading to a vanishingly small exclusion rate.

Similarly, species with no niche overlap should also coexist over long periods, regardless of how similar or dissimilar they are in competitive abilities (zone B, Fig. 2a). Exclusion rate will thus be zero when similarity in resource preference (niche overlap) is zero or competitive similarity equals 1, and indeed it will also be zero for a range of parameters near these limits, where classical deterministic coexistence occurs (zone C). However, in deterministic communities even minor niche overlap can lead to competitive exclusion when dissimilarity in competitive ability is high (zone B), and even minor differences in competitive ability can result in rapid exclusion if niche overlap is great (zone A). Zone D portrays a range of scenarios with varying degrees of competitive similarity and niche overlap. Depending on both factors, the resulting exclusion rates in this zone are highly variable. Finally, a very rapid exclusion is expected for scenarios with high niche overlap combined with clear competitive dominance (zone E in Fig. 2a). Presumably, such scenarios are uncommon in nature, given the high rate of exclusion (Adler et al. 2007).

It is plausible that, in many cases, similarities in niche requirements and in competitive ability are correlated. For example, niche requirements are highly heritable (Wiens and Graham 2005), as are many factors relating to competitive abilities (e.g. body size or growth form), such that close relatives are likely to be similar in both. Such species pairs are near the neutral corner of parameter space with slow exclusion at best. As noted above, species pairs with high niche

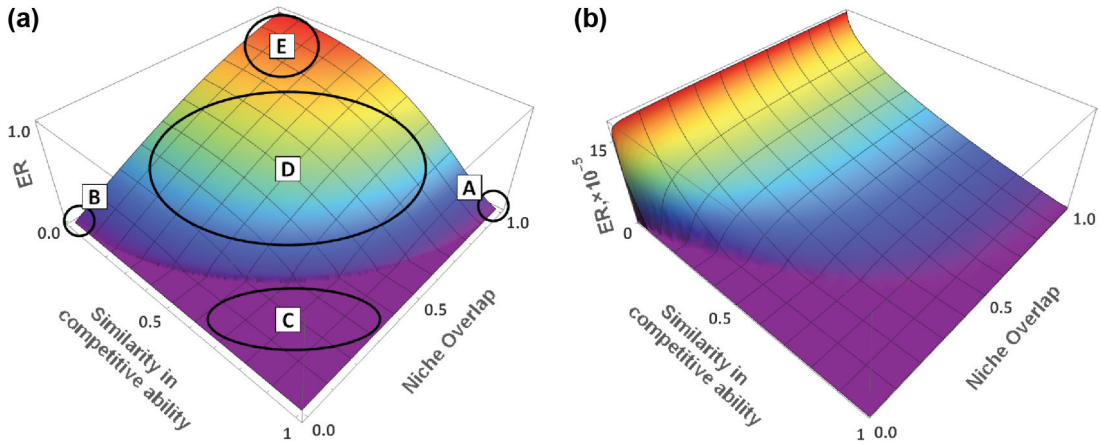


Figure 2. (a) A conceptual scheme for how exclusion rate (ER) should vary as a function of niche similarity and similarity in competitive ability. Point A represents the location of a neutral model. (b) The exclusion rate calculated for a two species – two resources model. Full details and parameter values are given in the appendix.

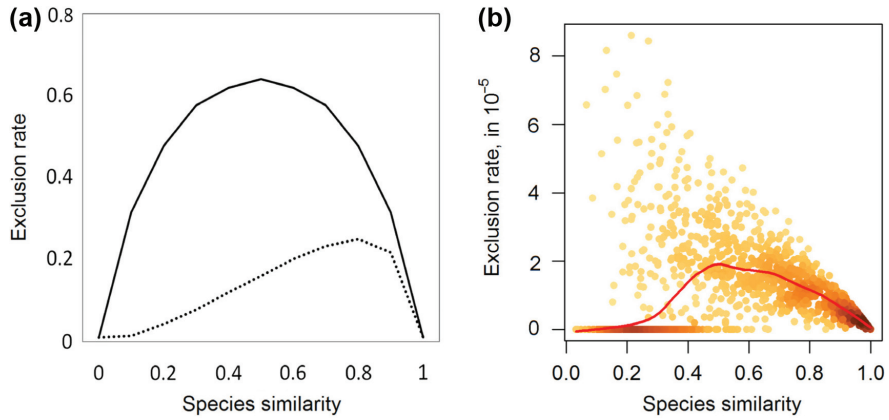


Figure 3. (a) Possible shapes of the relationship between exclusion rate and species similarity, where niche similarity and similarity in competitive ability are correlated. The solid line represents a scenario where competition severity and exclusion efficiency are both convex functions of overall species similarity. In the dotted line, competition severity is a concave (exponential) function of niche similarity. (b) Calculated exclusion rate calculated for 1000 randomly selected pairs of species in a two-species – two resource model. Full details and parameter values are given in the Supplementary material Appendix 4. The red line gives a lowess fit, which is qualitatively similar to lines in panel (a), and the points are colored according to a locally smoothed point density (darker means higher density) .

overlap and strong competitive dominance are unlikely to coexist in nature. More commonly, the more disparate are species' niches, the larger would be competitive differences between them in any specific environment. In such cases, where both aspects of similarity are partially correlated, we can combine these two components of competitive exclusion into a general notion of species similarity. Exclusion rate then becomes a hump-shaped function of the similarity between species (Fig. 3a). The exact shape of this function depends on the shape of both component functions and may vary substantially (dotted line in Fig. 3a). However, the two extreme cases, namely near-zero exclusion for non-competing species, as well as for highly similar species, should be a general feature of competitive exclusion.

## Case study – a consumer–resource model

A rich body of theoretical and empirical studies confirms the positive relation between species similarity and competition severity, but the negative relation between species similarity and exclusion rate has seldom been studied. In order to study the effects of niche overlap (NO) and competitive similarity (CS) concurrently, we employ a well-known model where two species compete for two resources (MacArthur 1970, Chesson 1990). We begin by considering a deterministic version of the model, before discussing how demographic stochasticity generalizes our conclusions. A detailed description of the model appears in Box 1.

The species differ in their consumption rates of the two resources. Niche overlap describes the similarity in resource preference, which determines the severity of competition. Competitive ability describes the ability to maximize the growth rate without changing niche overlap. In a consumer–resource model, this is determined by the overall magnitude of the rates at which the species consume resources, and convert them into biomass. The definitions of niche overlap and competitive similarity introduced by Chesson (Chesson 1990, 2000) and generalized by Carroll and co-authors (Carroll et al. 2011, Carroll and Nisbet 2015) cannot be applied to the model considered here (Supplementary material Appendix 1). For the sake of simplicity and clear interpretation, we adopt the following definitions of competitive similarity (CS) and niche overlap (NO):

$$CS = \min\left(\frac{K_{A1}K_{A2}}{K_{B1}K_{B2}}, \frac{K_{B1}K_{B2}}{K_{A1}K_{A2}}\right) \qquad NO = \min\left(\frac{K_{A1}/K_{A2}}{K_{B1}/K_{B2}}, \frac{K_{B1}/K_{B2}}{K_{A1}/K_{A2}}\right)$$

where $K_{A1}$ is the per capita rate at which species A consumes resource 1, $K_{A2}$ is the per capita rate at which species A consumes resource 2, etc. Both definitions have quite simple interpretations. We can think of $K_{A1} \times K_{A2}$ as the competitive ability of species A, i.e. a summary of its ability to consume both resources. CS is then the competitive ability of the weaker competitor divided by the competitive ability of the stronger competitor. With this definition, we have $0 \leq CS \leq 1$, with $CS = 1$ only when the two species have the same competitive ability, and CS close to 0 when the competitive abilities are very different. Note that we could have used any monotonic transformation of $K_{A1}K_{A2}$, such as $\sqrt{K_{A1}K_{A2}}$ or $\log(K_{A1}K_{A2})$, as our definition of competitive ability; we would, however, still be able to define CS in such a way that it was just a nonlinear transformation of the expression given above, so that our arguments and conclusions would be unchanged.

By contrast, niche overlap depends not on the overall consumption rates, summarized by their competitive ability, but on the ratio of consumption coefficients, e.g. $K_{A1}/K_{A2}$ for species A, which we call that species' resource preference. This expression for niche overlap is then the ratio of the species' resource preferences, with the "min" function ensuring this is a number between 0 and 1. We only have $NO = 1$ when the species have the same resource preferences (i.e. when the proportionate usage of the two resources by species A is the same as for species B). In the Supplementary material Appendix 1 we show that, under some simplifying assumptions about the model parameter values, the exclusion dynamics is determined completely by CS and NO as defined above. This simple model, and these definitions of

## Box 1. The model

A two-consumer – two-resource model is perhaps the simplest framework for exploring the effects of both niche overlap and competitive imbalance. In a consumer–resource model, competition takes place naturally through explicit depletion of shared resources. In order to explore competitive differences there must be at least two competing species, and in order to model niche differences we need at least two resources (because with only one resource the two species effectively occupy the same niche). Species $i \in \{A, B\}$ consumes resource $j \in \{1,2\}$ at per capita rate $K_{ij}$, and dies at rate $\mu_i$. Resource $j \in \{1,2\}$ undergoes monomolecular dynamics, being created at rate $c_j$ and dying (or degrading naturally) at rate $d_j$. If $A$, $B$ represent the densities of the consumer species, and $Q_1$, $Q_2$ the densities of the resources, then the model is described by the following equations:

$$\frac{dA}{dt} = A\left(K_{A1}Q_1 + K_{A2}Q_2 - \mu_A\right); \qquad \frac{dB}{dt} = B\left(K_{B1}Q_1 + K_{B2}Q_2 - \mu_B\right)$$

$$\frac{dQ_1}{dt} = c_1 - Q_1\left(AK_{A1} + BK_{B1} + d_1\right); \qquad \frac{dQ_2}{dt} = c_2 - Q_2\left(AK_{A2} + BK_{B2} + d_2\right)$$

Equations of this type are often used to describe a chemostat, in which case 'mortality' represents washout from the vessel and parameters $\mu_A$, $\mu_B$, $d_1$ and $d_2$ are taken to be equal. However, they can equally well be used to represent a more generic situation where resources are regenerated and degraded at a constant rate, in which case these parameters need not be equal. We assume the resource dynamics to be "fast", so that at any given moment of time they are at equilibrium, i.e. $\frac{dQ_1}{dt} = 0$, and $\frac{dQ_2}{dt} = 0$. We also make the following simplifying assumptions regarding parameter values: 1) $d_1 = d_2 = 0$, i.e. the natural death of resources is negligible compared to their consumption by species A and B; 2) $c_2 = c_2 = c$; 3) $\mu_A = \mu_B = \mu$. Thus, after the simplification, the dynamics of species is described by the following equations:

$$\frac{dA}{dt} = A\left(\frac{c\,K_{A1}}{AK_{A1} + BK_{B1}} + \frac{c\,K_{A2}}{AK_{A2} + BK_{B2}} - \mu\right); \quad \frac{dB}{dt} = B\left(\frac{c\,K_{B1}}{AK_{A1} + BK_{B1}} + \frac{c\,K_{B2}}{AK_{A2} + BK_{B2}} - \mu\right)$$

niche overlap and competitive similarity, are ideally suited to illustrating our ideas. However, these definitions can be extended to more general models, for example where N species compete for resources (see Supplementary material Appendix 2 for definitions of CS and NO in such models).

Calculations of the exclusion rate in this model, shown in Fig. 2b (also Supplementary material Appendix 3 for details), qualitatively support the conceptual predictions presented in Fig. 2a when the competitive similarity is substantially above zero. In particular, exclusion rate decreases with competitive similarity (for constant niche overlap), increases with niche overlap (for constant competitive similarity), and is zero when niche overlap is close to zero or competitive similarity is close to one. However, when competitive similarity approaches zero the exclusion rate from the model remains at a high value for all levels of niche overlap ($NO > 0$), rather than falling at low niche overlap as predicted in Fig. 2a. This is because, in the model, $CS = 0$ means that one species is infinitely better in consuming both resources than the other species. This leads to a complete devastation of resources for the less competitive species, which then disappears at its natural death rate independently of niche overlap. As discussed in Supplementary material Appendix 4, this behavior might not occur with other models or with different definitions of competitive similarity and niche overlap.

If areas with positive and zero exclusion rate in Fig. 2b are projected (flattened) on the plane of competitive similarity and niche overlap, the resulting figure will appear almost identical to two-dimensional coexistence plots shown in previous studies (May 1974, Chesson 1990, Adler et al. 2007, Carroll et al. 2011) with the only difference that here all possible values of competitive similarity are taken into account. However, in contrast to past studies, the calculation of exclusion rates allows us to model community dynamics and coexistence patterns that persist over finite (and therefore realistic) time spans. During finite time intervals, when examining real communities in flux, it is impossible to differentiate species coexisting in the classical sense from those that coexist only temporarily due to very slow competitive exclusion. This suggests that in the modelling of real communities it is important to consider mechanisms that slow down exclusion, in addition to mechanisms that promote indefinite coexistence.

The study of the exclusion rate also allows us to consider species' dynamics beyond the deterministic case. When demographic stochasticity is included (Supplementary material Appendix 5), all species face $> 0$ extinction risk, blurring the boundaries between deterministic coexistence and slow exclusion. The deterministic coexistence criterion with binary outcome does not provide a satisfactory description of such scenario. Instead, the exclusion rate of the species with stochastic influence can be estimated, as shown in Fig. 4. Interestingly, as the degree of demographic stochasticity rises (from panel a to c), the overall speed of exclusion rises and the 'plain' of deterministic coexistence is first blurred and then erased entirely. At very high demographic stochasticity, coexistence becomes restricted to cases of low niche overlap.

Figure 3b shows the computed model exclusion rate as a function of species similarity, for randomly generated pairs of species where niche overlap and competitive similarity

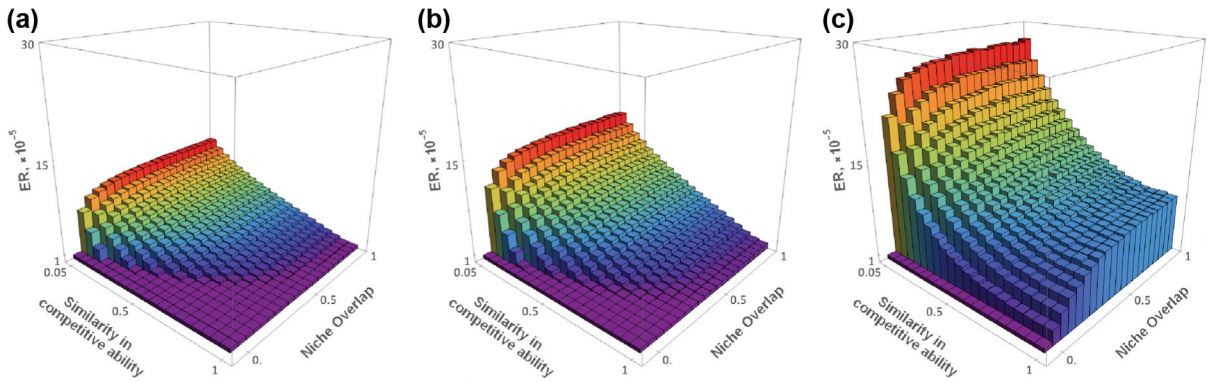


Figure 4. The effect of demographic stochasticity on exclusion rate. Populations with density $B_0$ of the superior species $B$ at equilibrium are shown: (a) $B_0 = 2000$; (b) $B_0 = 200$; (c) $B_0 = 20$. Simulations were conducted using the Gillespie algorithm (Gillespie 1977), the initial values $A = B = B_0/2$ were used. Competitive similarity and niche overlap take discrete values in the intervals (0.05, 1) and (0, 1) respectively with the step 0.05. Exclusion rate is obtained as the inverse of the mean exclusion time, 5000 different realizations of the demographic noise were used to obtain mean exclusion time for each value of competitive similarity and niche overlap.

are correlated. Full details of the sampling method and measure of species similarity are given in the Supplementary material Appendix 4. As in the conceptual prediction in Fig. 3a, the calculations show that exclusion rate goes to zero when species are completely different or completely similar (species similarity = 0 or 1), and is maximal at intermediate differences. As discussed in the Supplementary material Appendix 4, it turns out that the exclusion rate would not necessarily approach zero when species similarity approaches zero, unless we assume there is a tradeoff that prevents one species from being overwhelmingly better at consuming both resources than the other species. This is due to the high exclusion rate in the model when competitive similarity is zero, for any level of niche overlap, as illustrated in Fig. 2b. The exact shape of the relationship between species similarity and exclusion rate (e.g. Fig. 3b) depends on the nature of the correlation between niche overlap and competitive similarity, making this a critical issue for empirical research.

## Discussion

The novelty in our approach is that we explore the impact of niche overlap and similarity in competitive abilities on exclusion rate (operationally defined as 1/time to exclusion) rather than treating exclusion as a binary state. This is a crucial distinction. Neutral models (Hubbell 2001) have demonstrated that non-equilibrium coexistence can allow the accumulation of substantial competitive communities, so long as the rate of exclusion is sufficiently low. While these mechanisms were sometimes dismissed (Chesson 2000), their potential importance is now much more widely appreciated (Rosindell et al. 2012). Using exclusion rate as our dependent variable thus allows us to bring together niche perspectives (with equilibrium coexistence equating to zero rates) and neutral scenarios (with nearly zero exclusion rates) in a single framework. In stochastic conditions and with finite populations, we show that the distinction is blurred further: even populations that ought to coexist at equilibrium face risks of extinction.

We propose that the rate of competitive exclusion is a function of similarity in competitive abilities as well as of niche overlap. By dividing the concept of species similarity into these two components, we are then able to explore how the two factors combine to affect exclusion rates. The model explored here suggests strongly interacting effects. When competitive similarity is close to 1, niche overlap may be effectively irrelevant: complete niche overlap produces an effectively neutral scenario with zero or near-zero exclusion rates, whereas lower niche overlap results in equilibrium coexistence. If competitive similarity is somewhat lower, niche overlap becomes critical in determining coexistence, with exclusion rates rising strongly with increasing niche overlap. However, as competitive similarity approaches zero, the importance of niche overlap falls once again, as rapid competitive exclusion occurs for virtually any level of niche overlap ($> 0$). Adler et al. (2007) also explored the joint effects of niche and competitive ("fitness") differences on coexistence (indeed, their Fig. 2 closely parallels the lower 'coastal plain' in our Fig. 2), but they modelled only stable coexistence, and so could not explore the dynamics of the non-equilibrium cases (further 'inland'). Abrams (1998) used a consumer–resource model to show that competition can have strong effects even when competitive similarity is high and niche overlap is small, due to "biotic" (i.e. self-replenishing) resources being eradicated by apparent competition. However, he was considering the impact of competition on equilibrium densities when species coexist stably, so his results are consistent with zero exclusion rate in region C in our Fig. 2b.

One striking aspect of our model outcomes (Fig. 2b) is worth noting: while both competitive similarity and niche overlap affect the prospects of equilibrium coexistence (the 'plain' of 0 exclusion rates), in those non-equilibrium regions where exclusion rate is $> 0$, the relative importance of competitive similarity often exceeds that of niche overlap. Increasing niche overlap has relatively little impact on exclusion rates except for close to the threshold between exclusion and coexistence, but decreasing competitive similarity speeds up exclusion in virtually all cases. Our results suggest that 'slow exclusion' scenarios, where competitors

coexist over long periods despite being predicted to exclude one another, will be restricted almost exclusively to cases of very similar competitive abilities, regardless of the degree of niche overlap. It appears that to understand competitive exclusion we should focus at least as much attention on competitive similarity as on niche relations; yet the classical competition literature has largely been devoted to exploring effects of niche overlap (e.g. "limiting similarity", MacArthur and Levins 1967), whereas the effects of differences in competitive ability have been much less well explored (but see Aarssen 1983, Abrams 1986). However, introducing demographic stochasticity into our models elevates exclusion rates, except where niche overlap is near zero. Thus in highly stochastic dynamics (i.e. in tiny populations), niche overlap may once again take pride of place as the main factor determining coexistence.

Niche overlap and competitive similarity can be thought of as two aspects of a more general concept of species similarity. Accounting for the contrasting impact of these two factors on exclusion rate may result in very low exclusion rates not only for dissimilar species, but also for very similar species. Given a strong correlation between the two factors in nature, the highest rates of competitive exclusion may occur at intermediate levels of similarity, a possibility suggested but not tested by Keddy (1989). This modified form of the competitive exclusion principle is corroborated by findings of a very few empirical (Beaudrot et al. 2013) and modeling (Scheffer and Van Nes 2006) studies. The paucity of such studies may be due to the contradiction between this proposition and the prevailing perception of competitive exclusion. The notion that competitive exclusion does not prevent similar species from coexisting locally is not easy to accept since it is at odds with a large body of literature built upon a different conception of the exclusion process. Alternatively, the correlation between niche overlap and competitive similarity in nature may differ from that modelled here; the issue is a fertile topic for future empirical research.

One paradox which a generalized competitive exclusion principle may solve is the fact that a clear majority of studies reveal that phylogenetically similar species coexist more than expected by chance (Vamosi et al. 2009). As noted above, phylogenetic similarity often implies niche similarity (Wiens and Graham 2005). Given the traditional conception of competitive exclusion, phylogenetically similar species should coexist less frequently than phylogenetically dissimilar species. However, phylogenetic similarity is likely to enhance competitive similarity (as well as niche overlap). Thus, if competitive exclusion among competitively similar species is slow, as is proposed here, then there is less restriction on phylogenetically similar species to coexist.

Niche theory has long been struggling with the apparent contradiction between the notion that 'complete competitors cannot coexist' and the actual coexistence of a multitude of similar species in species-rich communities such as in tropical forests (Janzen 1970) and plankton (Hutchinson 1961). The modified competitive exclusion principle developed here allows a variety of outcomes to result from competitive interactions. Most importantly, it illuminates how similar competitors can coexist over long periods of time even without assuming external mechanisms. This revision may have far-reaching consequences for our notions of community structure and its determinants. New models can be built that describe the emergence of species-rich communities in terms of both competition severity and exclusion efficiency. This may lead to a richer appreciation of the mechanisms enabling coexistence without invoking the unrealistic assumptions of neutral theory.

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## References

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. – Am. Nat. 122: 707–731.
Abrams, P. A. 1986. The competitive exclusion principle: other views and a reply. – Trends Ecol. Evol. 1: 131–132.
Abrams, P. A. 1998. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer–resource systems. – Am. Nat. 152: 114–128.
Adler, P. B. et al. 2007. A niche for neutrality. – Ecol. Lett. 10: 95–104.
Allouche, O. and Kadmon, R. 2009. Demographic analysis of Hubbell's neutral theory of biodiversity. – J. Theor. Biol. 258: 274–280.
Beaudrot, L. et al. 2013. Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest among distantly related species. – Oecologia 173: 1053–1062.
Brown, W. L. and Wilson, E. O. 1956. Character displacement. – Syst. Zool. 5: 49–64.
Carroll, I. and Nisbet, R. 2015. Departures from neutrality induced by niche and relative fitness differences. – Theor. Ecol. 8: 449–465.
Carroll, I. et al. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. – Ecology 92: 1157–1165.
Chesson, P. L. 1982. The stabilizing effect of a random environment. – J. Math. Biol. 15: 1–36.
Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. – In: Freedman, H. I. and Strobeck, C. (eds), Population biology. Springer, pp. 188–198.
Chesson, P. L. 1990. MacArthur's consumer–resource model. – Theor. Popul. Biol. 37: 26–38.
Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.
Chisholm, R. A. and Pacala, S. W. 2010. Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. – Proc. Natl Acad. Sci. USA 107: 15821–15825.
Chisholm, R. A. and Pacala, S. W. 2011. Theory predicts a rapid transition from niche-structured to neutral biodiversity patterns across a speciation-rate gradient. – Theor. Ecol. 4: 195–200.
Colwell, R. and Futuyama, D. 1971. Ecology: on measurement of niche breadth and overlap. – Ecology 52: 567–576.
Connolly, S. R. et al. 2014. Commonness and rarity in the marine biosphere. – Proc. Natl Acad. Sci. USA 111: 8524–8529.
Darwin, C. 1859. On the origin of species. – John Murray, London.

Dayan, T. and Simberloff, D. 2005. Ecological and community-wide character displacement: the next generation. – Ecol. Lett. 8: 875–894.
Dybzinski, R. and Tilman, D. 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. – Am. Nat. 170: 305–318.
Fisher, C. K. and Mehta, P. 2014. The transition between the niche and neutral regimes in ecology. – Proc. Natl Acad. Sci. USA 111: 13111–13116.
Gause, G. F. 1932. Experimental studies on the struggle for existence. I. Mixed population of two species of yeast. – J. Exp. Biol. 9: 389–402.
Gillespie, J. H. 1977. Natural selection for variance in offspring numbers: a new evolutionary principle. – Am. Nat. 111: 1010–1014.
Gravel, D. et al. 2006. Reconciling niche and neutrality: the continuum hypothesis. – Ecol. Lett. 9: 399–409.
Grinnell, J. 1904. The origin and distribution of the chest-nut-backed chickadee. – Auk 21: 364–382.
Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – Biol. Rev. 52: 107–145.
Haegeman, B. and Etienne, R. S. 2011. Independent species in independent niches behave neutrally. – Oikos 120: 961–963.
Haegeman, B. and Loreau, M. 2011. A mathematical synthesis of niche and neutral theories in community ecology. – J. Theor. Biol. 269: 150–165.
Hardin, G. 1960. The competitive exclusion principle. – Science 131: 1292–1297.
Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). – Princeton Univ. Press.
Huisman, J. and Weissing, F. J. 1999. Biodiversity of plankton by species oscillations and chaos. – Nature 405: 407–410.
Hutchinson, G. E. 1941. Ecological aspects of succession in natural populations. – Am. Nat. 75: 406–418.
Hutchinson, G. E. 1961. The paradox of the plankton. – Am. Nat. 95: 137–145.
Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.
Kalmykov, L. V. and Kalmykov, V. L. 2013. Verification and reformulation of the competitive exclusion principle. – Chaos Solitons Fractals 56: 124–131.
Kalyuzhny, M. et al. 2014. Niche versus neutrality: a dynamical analysis. – Am. Nat. 184: 439–446.
Kalyuzhny, M. et al. 2015. A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. – Ecol. Lett. 18: 572–580.
Keddy, P. A. 1989. Competition. – Chapman and Hall.
Kramer, A. M. and Drake, J. M. 2014. Time to competitive exclusion. – Ecosphere 5: 1–16.
Lawlor, L. R. and Maynard-Smith, J. 1976. The coevolution and stability of competing species. – Am. Nat. 110: 79–99.
Leibold, M. A. 1999. Biodiversity and nutrient enrichment in pond plankton communities. – Evol. Ecol. Res. 1: 73–95.
Leibold, M. A. and McPeek, M. A. 2006. Coexistence of the niche and neutral perspectives in community ecology. – Ecology 87: 1399–1410.
Levin, B. 1969. A model for selection in systems of species competitionin. – In: Heinmets, R. (ed.), Concepts and models in biomathematics. Marcel Dekker, pp. 237–273.
Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. – Am. Nat. 104: 413–423.
MacArthur, R. 1970. Species packing and competitive equilibrium for many species. – Theor. Popul. Biol. 1: 1–11.
MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. – Am. Nat. 101: 377–385.
May, R. M. 1974. On the theory of niche overlap. – Theor. Popul. Biol. 5: 297–332.
Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.
Miller, S. R. et al. 2011. Dynamics of gene duplication in the genomes of chlorophyll d-producing cyanobacteria: implications for the ecological niche. – Genome Biol. Evol. 3: 601–613.
Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. – Folia Geobot. Phytotax. 29: 511–530.
Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of *Tribolium*. – Physiol. Zool. 27: 177–238.
Pianka, E. R. 1974. Niche overlap and diffuse competition. – Proc. Natl Acad. Sci. USA 71: 2141–2145.
Rosindell, J. et al. 2012. The case for ecological neutral theory. – Trends Ecol. Evol. 27: 203–208.
Roughgarden, J. 1976. Resource partitioning among competing species – a coevolutionary approach. – Theor. Popul. Biol. 9: 388–424.
Scheffer, M. and Van Nes, E. H. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. – Proc. Natl Acad. Sci. USA 103: 6230–6235.
Schoener, T. W. 1974. Resource partitioning in ecological communities. – Science 185: 27–39.
Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – J. Biogeogr. 12: 1–20.
Shtilerman, E. et al. 2015. Emergence of structured communities through evolutionary dynamics. – J. Theor. Biol. 383: 138–144.
Tilman, D. 1982. Resource competition and community structure. – Princton Univ. Press.
Tilman, D. and Wedin, D. 1991. Oscillations and chaos in the dynamics of a perennial grass. – Nature 353: 653–655.
Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. – Blackwell Science.
Turner, P. E. et al. 1996. Tests of ecological mechanisms promoting the stable coexistence of two bacterial genotypes. – Ecology 77: 2119–2129.
Vamosi, S. et al. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. – Mol. Ecol. 18: 572–592.
Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. – Nature 118: 558–560.
Wiens, J. and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology and conservation biology. – Annu. Rev. Ecol. Syst. 93: 456–461.
Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. – Oecologia 130: 1–14.
Yenni, G. et al. 2012. Strong self-limitation promotes the persistence of rare species. – Ecology 93: 456–461.
Zhang, D.-Y. and Lin, K. 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? – J. Theor. Biol. 188: 361–367.

Supplementary material (available online as Appendix oik-04380 at <www.oikosjournal.oorg/appendix/oik-04380>). Appendix 1–5.